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Research Article

Species diversity of *Tricholoma* (Agaricales, Tricholomataceae) from Shanxi Province of northern China with the description of four new species

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Abstract

Species of *Tricholoma* are of great economic and ecological value. There are many studies on *Tricholoma* worldwide, but the areas investigated are generally North America and Europe. There is limited knowledge about *Tricholoma* in China. In this study, 21 species of *Tricholoma* were confirmed in Shanxi Province based on morphological and molecular phylogenetic analyses. These species are located in eight sections, viz. sect. *Atrosquamosa*, sect. *Genuina*, sect. *Lasciva*, sect. *Matsutake*, sect. *Pardinicuti*, sect. *Rigida*, sect. *Terrea* and sect. *Tricholoma*. Of these, four species are described as new to science: *T. flavoviride*, *T. fumeobrunneum*, *T. parafulvum*, and *T. viscidum*.

Key words: Basidiomycota, ectomycorrhiza, phylogenetic analyses, taxonomy

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Introduction

Tricholoma (Fr.) Staude was erected as a genus in the year 1857 (Staude 1857). This genus is mainly characterized by fleshy basidiomata, adnexed to emarginate lamellae, a central stipe, white spore prints, subglobose to oblong basidiospores, simple pileipellis structures and often the absence of well-differentiated cystidia (Kost 1981; Singer 1986; Christensen and Noordeloos 1999; Bessette et al. 2013; Christensen and Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017; Reschke et al. 2018; Ding et al. 2023). Species of *Tricholoma* are ecologically and economically vital, not only for forming ectomycorrhizal symbioses with trees of the families Pinaceae, Betulaceae, Fagaceae, Salicaceae, Myrtaceae and Nothofagaceae, but also as famous delicacy mushrooms, such as *T. matsutake* (S. Ito & S. Imai) Singer and its allies (Bougher 1996; Chapela and Garbelotto 2004; Matsushita et al. 2005; Suzuki 2005; Tedersoo et al. 2010; Ota et al. 2012; Bessette et al. 2013; Christensen and Heilmann-Clausen 2013; Sánchez-García and Matheny 2016; Heilmann-Clausen et al. 2017; Reschke et al. 2018; Ding et al. 2023). Based on morphological and molecular approaches, a number of infrageneric classifications of *Tricholoma* have been proposed (Bon 1984, 1991; Singer 1986; Riva 1988, 2003; Christensen and Noordeloos 1999; Noordeloos and Christensen 1999; Christensen and Heilmann-Clausen 2008;

Reschke et al. 2018; Landry et al. 2022; Trudell et al. 2022; Ding et al. 2023). For example, Ding et al. (2023) assessed subgenera and section boundaries within *Tricholoma* by using morphology and phylogenetic evidence from 50-locus, in which a total of four subgenera and 11 sections were identified.

Recently, some important taxonomic works have been focused on *Tricholoma* in China (Cui et al. 2022; Ding et al. 2023; Yang et al. 2023). However, our knowledge of *Tricholoma* is significantly insufficient in Shanxi Province. During the last seven years, we collected a lot of specimens of *Tricholoma* in this region. Our morphological examinations and molecular analyses based on these collections showed they represented 21 species, including four undescribed species. The aim of this paper is to describe these new species and clarify the species diversity and geographic distribution of *Tricholoma* in Shanxi Province, northern China.

Materials and methods

Morphological studies

Collections were obtained and photographed in the field from Shanxi Province, North China, dried in a fruit drier at 40–45 °C, and deposited at BJTC (Herbarium Biology Department, Capital Normal University) and HSA (Herbarium of Shanxi Institute for Functional Foods, Shanxi Agricultural University). Macroscopic characters were recorded from fresh specimens. Standardized color values matching the color of the description were taken from ColorHexa (http://www.colorhexa.com/). Microscopic characteristics were observed in sections obtained from dry specimens mounted in 5% KOH, Congo Red, or Melzer's reagent (Dring 1971). Dimensions of basidiospores are given using the following format '(a–)b–c(–d)', where the range 'b–c' represents at least 90% of the measured values, and 'a' and 'd' are the most extreme values. 'Q' refers to the length/width ratio of basidiospores in the side view.

DNA extraction, PCR amplification, and DNA sequencing

A small amount of basidiomata material (20–30 mg) was crushed by shaking for 45 seconds at 30 Hz 2–4 times (Mixer Mill MM301, Haan, Germany) in a 1.5 mL tube, together with a 3 mm diam. tungsten carbide ball. Total genomic DNA was extracted from the powdered basidiomata using NuClean Plant Genomic DNA Kit (CWBIO, Beijing, China), following the manufacturer's instructions. The ITS region was amplified using the primers ITS1-F/ITS4 (White et al. 1990; Gardes and Bruns 1993). Polymerase Chain Reactions (PCR) for ITS region was performed in 25 µl reaction containing 2 µl DNA template, 1 µl primer (10 µM) each, 12.5 µl of 2 × Master Mix [Tiangen Biotech (Beijing) Co.], 8.5 µl ddH2O. PCR reactions were implemented as follows: an initial denaturation at 94 °C for 5 min; then 35 cycles of the following denaturation at 94 °C for 30 s, annealing at 55 °C for 45 s, 72 °C for 1 min; and a final extension at 72 °C for 10 min. The PCR products were sent to Beijing Zhongkexilin Biotechnology Co. Ltd. (Beijing, China) for purifying, sequencing, and editing. Accession numbers of new and downloaded sequences stored in the NCBI database are provided in Table 1.

Table 1. Specimens used in ITS phylogenetic analysis and their GenBank accession numbers. Newly generated sequences are in bold.

Taxon name	Specimen voucher	Origin	ITS
Leucopaxillus laterarius	KUN-HKAS 106319	China	MW724394
Leucopaxillus tricolor	MB 000946	Germany	MW724429
Tricholoma albobrunneum	MC99-060	France	LT000077
Tricholoma albobrunneum	KUN-HKAS 68189	China	MW724479
Tricholoma album	MC95-159	Denmark	LT000008
Tricholoma album	MB 006366	Germany	MW724416
Tricholoma album	MB 006323	Germany	MW724421
Tricholoma ammophilum	WTU-F-073083	USA	MW597140
Tricholoma ammophilum	WTU-F-073015	USA	MW597199
Tricholoma ammophilum	**HSA 371**	**China**	**PQ499533**
Tricholoma argyraceum	MEN9491	Netherlands	LT000198
Tricholoma argyraceum	**BJTC FM2197**	**China**	**PQ499519**
Tricholoma argyraceum	**BJTC FM2372**	**China**	**PQ499520**
Tricholoma atrosquamosum	**BJTC FM4346**	**China**	**PQ499525**
Tricholoma aurantium	MC97-227	Denmark	LT000012
Tricholoma aurantium	**BJTC FM2193**	**China**	**PQ499534**
Tricholoma aurantium	**BJTC FM2195**	**China**	**PQ499535**
"Tricholoma auratum"	Tk1	Japan	AB289663
"Tricholoma auratum"	ISK1	Japan	AB289662
Tricholoma badicephalum	UBC-F-16235r	Canada	MW597207
Tricholoma badicephalum	WTU-F-073095	USA	MW597309
Tricholoma bakamatsutake	TNS:F-12866	Japan	AB699654
Tricholoma bakamatsutake	KUN-HKAS 106313	China	MW724402
Tricholoma bakamatsutake	KUN-HKAS 107570	China	MW724468
Tricholoma bakamatsutake	**BJTC FM3440**	**China**	**PQ499506**
Tricholoma bakamatsutake	**BJTC FM3441**	**China**	**PQ499507**
Tricholoma basirubens	MC01-209	Croatia	LT000001
Tricholoma basirubens	TL5303	Sweden	LT000158
Tricholoma batschii	KMS436	USA	AF377238
Tricholoma batschii	MB-003027	Germany	MF034298
Tricholoma bonii	LUG-F8450	Italy	LT000101
Tricholoma bonii	HMJAU35946	China	MW724393
Tricholoma bonii	**BJTC FM1280**	**China**	**PQ499508**
Tricholoma bonii	**BJTC FM1388**	**China**	**PQ499509**
Tricholoma bonii	**BJTC FM920**	**China**	**PQ499510**
Tricholoma boudieri	HKAS97070	China	MW724437
Tricholoma boudieri	HKAS97163	China	MW724373
Tricholoma boudieri	**BJTC FM1528**	**China**	**PQ499521**
Tricholoma boudieri	**BJTC FM2752**	**China**	**PQ499522**
Tricholoma cingulatum	MC96-134	Denmark	LT000015
Tricholoma cingulatum	**BJTC FM1172**	**China**	**PQ499516**
Tricholoma cingulatum	**BJTC FM820**	**China**	**PQ499517**
Tricholoma cingulatum	**BJTC FM1191**	**China**	**PQ499518**
Tricholoma citrinum	MB-305716	China	MF034262
Tricholoma citrinum	KUN-HKAS 71086	China	MW724356
Tricholoma colossus	MC97-047	Sweden	LT000164
Tricholoma colossus	MB-002363	Germany	MF034285
Tricholoma columbetta	MC95-181	Denmark	LT000017
Tricholoma columbetta	MQ20-HRL3139-QFB32663	Canada	MW628118
Tricholoma dulciolens	H:7002022	Sweden	AB738883
Tricholoma dulciolens	-	USA	AF309523

Taxon name	Specimen voucher	Origin	ITS
Tricholoma elegans	OTA:61947	New Zealand	JX178630
Tricholoma elegans	TENN:063711	New Zealand	KJ417316
Tricholoma equestre	MC94-027	Denmark	LT000018
Tricholoma equestre	MC96-155	Denmark	LT000020
Tricholoma equestre	HMJAU22249	Belarus	MW724392
"*Tricholoma equestre*"	MB305549	China	MF034257
"*Tricholoma equestre*"	MB305676	China	MF034261
"*Tricholoma equestre*"	MB-301506	China	MF034239
"*Tricholoma equestre*"	EqFrW	France	HM590874
Tricholoma filamentosum	C-F-35924	Sweden	LT000165
Tricholoma filamentosum	MB 000950 (KR9404)	Germany	MW724422
"*Tricholoma flavovirens*"	trh545	USA	AF458449
"*Tricholoma flavovirens*"	trh546	USA	AF458452
"*Tricholoma flavovirens*"	613	Japan	AB036895
"*Tricholoma flavovirens*"	KGP52	USA	DQ822834
Tricholoma flavoviride	**BJTC FM3966**	**China**	**PQ499559**
Tricholoma flavoviride	**BJTC FM4164**	**China**	**PQ499560**
Tricholoma flavoviride	**BJTC FM3512**	**China**	**PQ499561**
Tricholoma focale	JV97-239	Sweden	LT000166
Tricholoma focale	KUN-HKAS 106309	China	MW724460
Tricholoma forteflavescens	HKAS93511	China	MF034207
Tricholoma forteflavescens	MB-301985	China	MF034246
Tricholoma frondosae type I	MC95-130	Sweden	LT000167
Tricholoma frondosae type I	KUN-HKAS 98072	China	MW724365
Tricholoma frondosae type I	KUN-HKAS 87149	China	MW724346
Tricholoma frondosae type II	MC96-235	Denmark	LT000023
Tricholoma frondosae type II	MC00-225	Slovenia	LT000140
***Tricholoma frondosae* type II**	**BJTC FM2026**	**China**	**PQ499556**
***Tricholoma frondosae* type II**	**BJTC FM3895**	**China**	**PQ499557**
***Tricholoma frondosae* type II**	**BJTC FM4157**	**China**	**PQ499558**
Tricholoma fulvomaculatum	HKAS107572	China	MW724472
Tricholoma fulvomaculatum	HKAS107576	China	MW724473
Tricholoma fulvum	JHC04-251	Sweden	LT000171
Tricholoma fulvum	MQ20-YL-CMMF001495	Canada	MW627880
Tricholoma fumeobrunneum	**BJTC FM3445**	**China**	**PQ499552**
Tricholoma fumeobrunneum	**BJTC FM3436**	**China**	**PQ499553**
Tricholoma fumeobrunneum	**BJTC FM3571**	**China**	**PQ499554**
Tricholoma fumeobrunneum	**BJTC FM3574**	**China**	**PQ499555**
Tricholoma highlandense	HKAS70192	China	KY488549
Tricholoma highlandense	KUN-HKAS 107590	China	MW724452
Tricholoma ilkkae	S-F173364	Sweden	LT222028
Tricholoma ilkkae	S-F513823	Sweden	LT222029
"*Tricholoma joachimii*"	O-F167194	Norway	LT222022
Tricholoma imbricatum	KUN-HKAS 112559	China	MW724476
Tricholoma imbricatum	KUN-HKAS 87886	China	MW724327
Tricholoma imbricatum	**BJTC FM1170**	**China**	**PQ499549**
Tricholoma imbricatum	**BJTC FM1445**	**China**	**PQ499550**
Tricholoma imbricatum	**BJTC FM1446**	**China**	**PQ499551**
Tricholoma inocybeoides	MC03-229	Denmark	LT000025
Tricholoma inocybeoides	MC97-060	Sweden	LT000176
Tricholoma lascivum	MC00-519	Denmark	LT000028
Tricholoma lascivum	MB-303096	Ukraine	MF034316
Tricholoma lishanense	**BJTC FM1023**	**China**	**PQ499526**
Tricholoma lishanense	**BJTC FM1137**	**China**	**PQ499527**
Tricholoma lishanense	**BJTC FM1735**	**China**	**PQ499528**

Taxon name	Specimen voucher	Origin	ITS
Tricholoma matsutake	KUN-HKAS 98323	China	MW724385
Tricholoma matsutake	MC03-600	Sweden	LT000178
Tricholoma matsutake	TNS:F-12850	Japan	AB699630
Tricholoma murrillianum	SAT-16-319-01	USA	KY660032
Tricholoma murrillianum	NY586560	USA	LT220179
Tricholoma olivaceotinctum	MC97103	Sweden	FJ544861
Tricholoma olivaceotinctum	KUN-HKAS 107586	China	MW724405
Tricholoma olivaceum	HKAS93513	China	MF034209
Tricholoma olivaceum	KUN-HKAS 68600	China	MW724351
Tricholoma orienticolossus	HAKS99341	China	MT124443
Tricholoma orienticolossus	HAKS98045	China	MT124444
Tricholoma orientifulvum	HAKS107157	China	MT114682
Tricholoma orientifulvum	HAKS107156	China	MT124445
Tricholoma parafulvum	**BJTC FM2500**	**China**	**PQ499536**
Tricholoma parafulvum	**BJTC FM4065**	**China**	**PQ499537**
Tricholoma parafulvum	**BJTC FM4210**	**China**	**PQ499538**
Tricholoma pardinum	C-F-96190	USA	LT000142
Tricholoma pardinum	MB 006381	Germany	MW724424
Tricholoma pessundatum	JV04-482	Denmark	LT000032
Tricholoma pessundatum	MQ20-JLAB931-CMMF009347	Canada	MW628012
Tricholoma populinum	O-F63960	Norway	JN019594
Tricholoma populinum	KUN-HKAS 106657	China	MW724411
Tricholoma populinum	**BJTC FM1144**	**China**	**PQ499529**
Tricholoma populinum	**BJTC FM1145**	**China**	**PQ499530**
Tricholoma populinum	**BJTC FM1165**	**China**	**PQ499531**
Tricholoma populinum	**BJTC FM1979**	**China**	**PQ499532**
Tricholoma psammopus	MC04-600	Slovenia	LT000145
Tricholoma psammopus	KUN-HKAS 106302	China	MW724436
Tricholoma psammopus	**BJTC FM2673**	**China**	**PQ499546**
Tricholoma psammopus	**BJTC FM1405**	**China**	**PQ499547**
Tricholoma psammopus	**BJTC FM814**	**China**	**PQ499548**
Tricholoma qiaomianjun	KUN-HKAS 101303	China	OK036719
Tricholoma qiaomianjun	KUN-HKAS 115901	China	OK036720
Tricholoma roseoacerbum	MQ20-HRL1010a-QFB32619	Canada	MW628060
Tricholoma roseoacerbum	KUN-HKAS 88046	China	MW724332
Tricholoma rufobrunneum	KUN-HKAS49069	China	OL331894
Tricholoma rufobrunneum	KUN-HKAS90808	China	OL331895
Tricholoma saponaceum	C-F23337	Denmark	LT000038
Tricholoma saponaceum	JHC00-049	Norway	LT000123
Tricholoma saponaceum	MB-002941	Germany	MF034221
Tricholoma saponaceum	**BJTC FM2772**	**China**	**PQ499523**
Tricholoma saponaceum	**BJTC FM2773**	**China**	**PQ499524**
Tricholoma sinoacerbum	GDGM:44680	China	KT160219
Tricholoma sinoacerbum	KUN-HKAS 105349	China	MW724434
Tricholoma sinopardinum	KUN-HKAS 91129	China	MW724361
Tricholoma sinopardinum	HKAS82533	China	KY488552
Tricholoma smithii	DBG:CLO4513	USA	MG719957
Tricholoma sp.	HKAS106303	China	MW724450
Tricholoma sp.	HKAS101281	China	MW724443
Tricholoma squarrulosum	JHC93-224	Denmark	LT000047
Tricholoma squarrulosum	JHC93-262	Denmark	LT000048
Tricholoma stans	MC95-145	Sweden	LT000189
Tricholoma stans	KUN-HKAS 87940	China	MW724329
Tricholoma stiparophyllum	MC95-117	Sweden	LT000190
Tricholoma stiparophyllum	MQ20-GUE1522-CMMF014811	Canada	MW628089

Taxon name	Specimen voucher	Origin	ITS
Tricholoma sudum	JV96-306	Denmark	LT000050
Tricholoma sudum	MC98-601	Denmark	LT000051
Tricholoma terreum	MEN95192	Germany	LT000098
Tricholoma terreum	KUN-HKAS 69914	China	MW724459
Tricholoma terreum	**BJTC FM2414**	**China**	**PQ499511**
Tricholoma terreum	**BJTC FM3657**	**China**	**PQ499512**
Tricholoma terreum	**BJTC FM3677**	**China**	**PQ499513**
Tricholoma triste	E3754	Germany	LT000099
Tricholoma triste	**BJTC FM1269**	**China**	**PQ499514**
Tricholoma triste	**BJTC FM3817**	**China**	**PQ499515**
"Tricholoma ulvinenii"	JuV13229F	Finland	LT000068
"Tricholoma ulvinenii"	JuV26740F	Finland	LT000069
"Tricholoma ulvinenii"	IK931613	Finland	LT000067
Tricholoma umbonatum type I	MC00A01	Denmark	LT000063
Tricholoma umbonatum type II	TRgmb00651	Italy	LT000114
Tricholoma ustale	JHC92-299	Denmark	LT000064
Tricholoma ustale	MB-002924	Germany	MF034288
Tricholoma ustaloides	MC99-067	France	LT000094
Tricholoma ustaloides	MB-002929	Germany	MF034291
Tricholoma vaccinum	MC95-109	Sweden	LT000195
Tricholoma vaccinum	DBG:23466	USA	MF034272
Tricholoma vaccinum	KUN-HKAS 98065	China	MW724364
Tricholoma vaccinum	**BJTC FM937**	**China**	**PQ499543**
Tricholoma vaccinum	**BJTC FM943**	**China**	**PQ499544**
Tricholoma vaccinum	**BJTC FM1425**	**China**	**PQ499545**
Tricholoma venenatoides	WTU-F-073089	USA	MW597303
Tricholoma viscidum	**BJTC FM4198**	**China**	**PQ499539**
Tricholoma viscidum	**BJTC FM3388**	**China**	**PQ499540**
Tricholoma viscidum	**BJTC FM4038**	**China**	**PQ499541**
Tricholoma viscidum	**BJTC FM4199**	**China**	**PQ499542**

Phylogenetic analyses

For this study, the ITS dataset was compiled to identify the new species and to investigate their phylogenetic position in the *Tricholoma*. *Leucopaxillus tricolor* (Peck) Kühner and *Leucopaxillus laterarius* (Peck) Singer & A.H. Sm. were selected as outgroups based on previous studies (Ding et al. 2023). The sequences of the ITS were aligned in the online version of MAFFT 7.110 using default parameters (Katoh and Standley 2013) and manually edited in BioEdit v.7.0.9 (Hall 1999). The final alignments were submitted to TreeBASE 31776.

Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian inference (BI). ML analysis was carried out in RAxML 8.0.14 (Stamatakis 2014) with parameters at default settings using a GTRGAMMAI model. 1000 bootstrap replicates were computed in RAxML using a rapid bootstrap analysis and search for the best-scoring ML tree. BI analysis was performed in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The best-fitted substitution model for ITS was determined through MrModeltest v2.3 (Nylander 2004) by using the Akaike Information Criterion (AIC). GTR+I+G was chosen as the best model for ITS. We used two independent runs with four Markov chains Monte Carlo (MCMC) for 3 775 000 generations under the default settings. The average standard deviations of split frequency (ASDSF) values were far lower than 0.01 at the end of the runs. Trees were sampled every 100 generations after burn-in

(25% of trees were discarded as the burn-in phase of the analyses, set up well after convergence), and 50% of majority-rule consensus trees were constructed.

Clades with bootstrap support (MLBS) ≥ 70% and Bayesian posterior probability (BPP) ≥ 0.95 were considered significantly supported (Hillis and Bull 1993; Alfaro et al. 2003). All phylogenetic trees were viewed with TreeView (Page 2001).

Results

Phylogenetic analyses

The ITS dataset consisted of 191 sequences, including 56 sequences newly generated from our collections. The length of the dataset was 578 bp after the exclusion of poorly aligned sites. Our present analyses (Fig. 1) revealed that members of *Tricholoma* in this dataset formed a monophyletic lineage with high likelihood bootstrap support (MLB = 100%) and strong posterior probability support (BPP = 1.00). The sequences of our 56 collections formed 21 strongly support clades, indicating they were 21 distinct species, and these phylogenetic species were respectively placed in eight sections, i.e. sect. *Atrosquamosa*, sect. *Genuina*, sect. *Lasciva*, sect. *Matsutake*, sect. *Pardinicuti*, sect. *Rigida*, sect. *Terrea* and sect. *Tricholoma*. Of them, four species are described as new species (see Taxonomy in this paper), and the remaining 17 clades correspond well to the previously described species (also see the photos of their basidiocarps in Figs 4, 5).

Taxonomy

Tricholoma flavoviride **L. Fan, N. Mao & J.J Yang, sp. nov.**

MycoBank No: MB 856305

Figs 2A, B, 3A, C

Diagnosis. It is distinguished by the combination of the following features: greenish-yellow to yellowish-brown pileus, stipe surface with brownish fibrils, or reflexed squamules. It is most similar to *T. citrinum* Y.Y. Cui & Zhu L. Yang but differs by habitat associated with broadleaf forest.

Holotype. China • Shanxi Province, Pu County, Wulu Mountain, 36°33'34"N, 111°12'40"E, elev. 1510 m, on the ground in broadleaf forest dominated by *Quercus* sp., 28 September 2023, J.Z Cao, MS808 (BJTC FM4164), GenBank Acc. No.: ITS = PQ499560, mtSSU = PQ499564, *rpb2* = PQ509907, *mcm7* = PQ509917.

Etymology. *flavoviride* (Lat.): referring to the color of the basidiomata.

Description. ***Basidiomata*** small to medium-sized. ***Pileus*** 20–55 mm diam., at first hemispherical to convex, later plano-convex to applanate with age, with an umbo at center; surface dry, slightly viscid when wet, greenish-yellow (#dbd252) to yellowish-brown (#c2a677), center darker to dark brown (#7a614d) when mature, covered with brown (#b49976) squamules; margin incurved or not. ***Lamellae*** sinuate, crowded, greenish-yellow (#b4ae6c) to yellowish-brown (#d9c45b); lamellulae in 2–4 tiers, concolorous with lamellae. ***Stipe*** 32–70 mm long, 12–17 mm diam., cylindrical, equal or enlarge downwards, dry, white (#f9f9f8) at apex, pale yellow (#e7e1a5) to yellowish brown (#d7cb67) below, covered with brownish (#9c8c58) fibrils or reflexed squamules. ***Context*** white (#ffffff). ***Odor*** unrecorded. ***Taste*** not recorded.

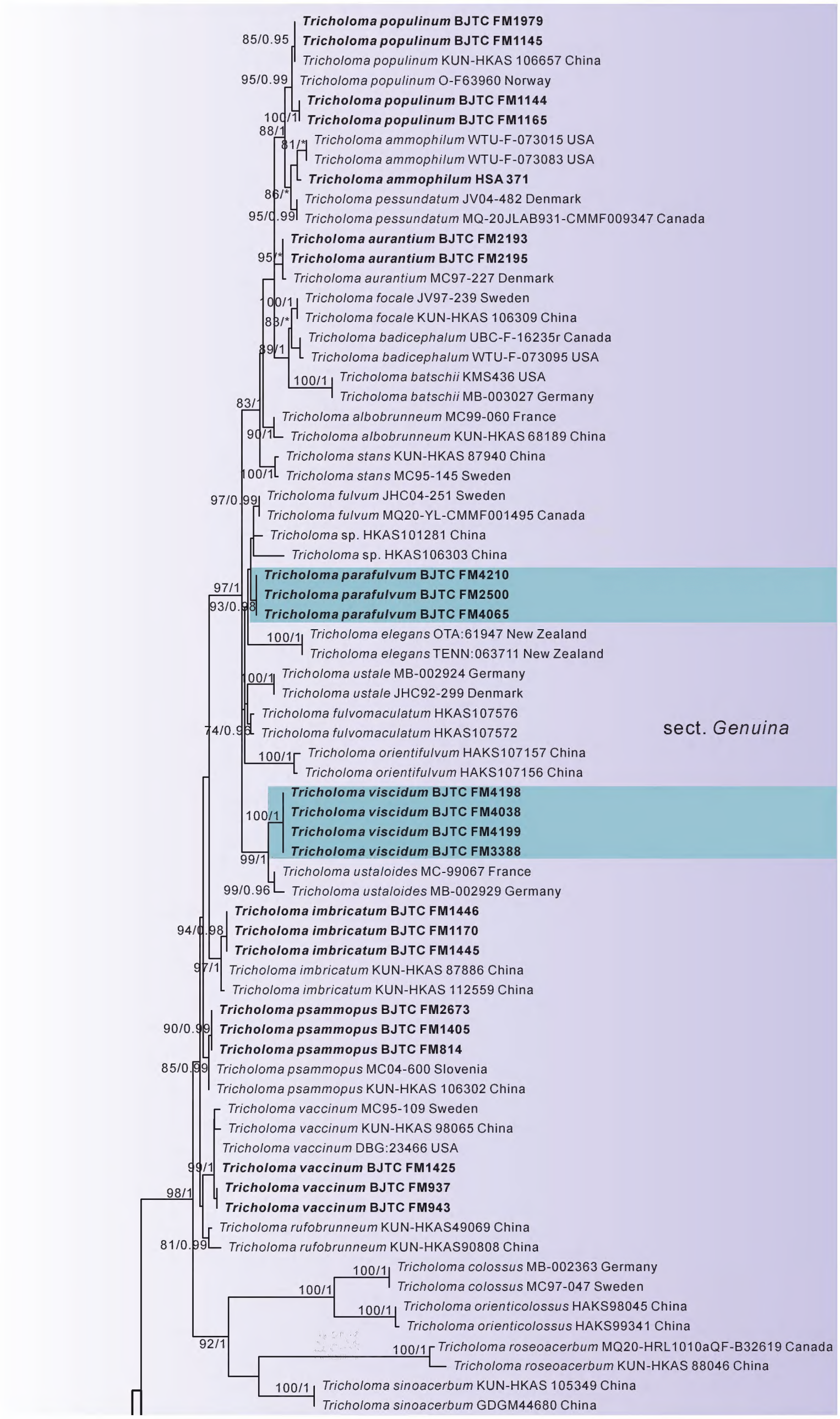
Tricholoma populinum BJTC FM1979
85/0.95 **Tricholoma populinum BJTC FM1145**
Tricholoma populinum KUN-HKAS 106657 China
95/0.99 *Tricholoma populinum* O-F63960 Norway
Tricholoma populinum BJTC FM1144
100/1 **Tricholoma populinum BJTC FM1165**
88/1
81/* *Tricholoma ammophilum* WTU-F-073015 USA
Tricholoma ammophilum WTU-F-073083 USA
Tricholoma ammophilum HSA 371
86/* *Tricholoma pessundatum* JV04-482 Denmark
95/0.99 *Tricholoma pessundatum* MQ-20JLAB931-CMMF009347 Canada
Tricholoma aurantium BJTC FM2193
95/* **Tricholoma aurantium BJTC FM2195**
Tricholoma aurantium MC97-227 Denmark
100/1 *Tricholoma focale* JV97-239 Sweden
88/* *Tricholoma focale* KUN-HKAS 106309 China
Tricholoma badicephalum UBC-F-16235r Canada
89/1 *Tricholoma badicephalum* WTU-F-073095 USA
100/1 *Tricholoma batschii* KMS436 USA
Tricholoma batschii MB-003027 Germany
83/1 *Tricholoma albobrunneum* MC99-060 France
90/1 *Tricholoma albobrunneum* KUN-HKAS 68189 China
Tricholoma stans KUN-HKAS 87940 China
100/1 *Tricholoma stans* MC95-145 Sweden
97/0.99 *Tricholoma fulvum* JHC04-251 Sweden
Tricholoma fulvum MQ20-YL-CMMF001495 Canada
Tricholoma sp. HKAS101281 China
Tricholoma sp. HKAS106303 China
Tricholoma parafulvum BJTC FM4210
97/1 **Tricholoma parafulvum BJTC FM2500**
93/0.98 **Tricholoma parafulvum BJTC FM4065**
100/1 *Tricholoma elegans* OTA:61947 New Zealand
Tricholoma elegans TENN:063711 New Zealand
100/1 *Tricholoma ustale* MB-002924 Germany
Tricholoma ustale JHC92-299 Denmark
Tricholoma fulvomaculatum HKAS107576
74/0.96 *Tricholoma fulvomaculatum* HKAS107572
sect. *Genuina*
100/1 *Tricholoma orientifulvum* HAKS107157 China
Tricholoma orientifulvum HAKS107156 China
Tricholoma viscidum BJTC FM4198
100/1 **Tricholoma viscidum BJTC FM4038**
Tricholoma viscidum BJTC FM4199
Tricholoma viscidum BJTC FM3388
99/1 *Tricholoma ustaloides* MC-99067 France
99/0.96 *Tricholoma ustaloides* MB-002929 Germany
Tricholoma imbricatum BJTC FM1446
94/0.98 **Tricholoma imbricatum BJTC FM1170**
Tricholoma imbricatum BJTC FM1445
97/1 *Tricholoma imbricatum* KUN-HKAS 87886 China
Tricholoma imbricatum KUN-HKAS 112559 China
Tricholoma psammopus BJTC FM2673
90/0.99 **Tricholoma psammopus BJTC FM1405**
Tricholoma psammopus BJTC FM814
85/0.99 *Tricholoma psammopus* MC04-600 Slovenia
Tricholoma psammopus KUN-HKAS 106302 China
Tricholoma vaccinum MC95-109 Sweden
Tricholoma vaccinum KUN-HKAS 98065 China
Tricholoma vaccinum DBG:23466 USA
99/1 **Tricholoma vaccinum BJTC FM1425**
98/1 **Tricholoma vaccinum BJTC FM937**
Tricholoma vaccinum BJTC FM943
Tricholoma rufobrunneum KUN-HKAS49069 China
81/0.99 *Tricholoma rufobrunneum* KUN-HKAS90808 China
100/1 *Tricholoma colossus* MB-002363 Germany
100/1 *Tricholoma colossus* MC97-047 Sweden
100/1 *Tricholoma orienticolossus* HAKS98045 China
Tricholoma orienticolossus HAKS99341 China
92/1
100/1 *Tricholoma roseoacerbum* MQ20-HRL1010aQF-B32619 Canada
Tricholoma roseoacerbum KUN-HKAS 88046 China
100/1 *Tricholoma sinoacerbum* KUN-HKAS 105349 China
Tricholoma sinoacerbum GDGM44680 China

Figure 1. Phylogenetic tree generated from a maximum likelihood analysis based on ITS sequences, showing the phylogenetic relationships of *Tricholoma*. Numbers representing likelihood bootstrap support (MLB ≥ 70%, left) and significant Bayesian posterior probability (BPP ≥ 0.95, right) are indicated above the nodes. Novel sequences are printed in bold.

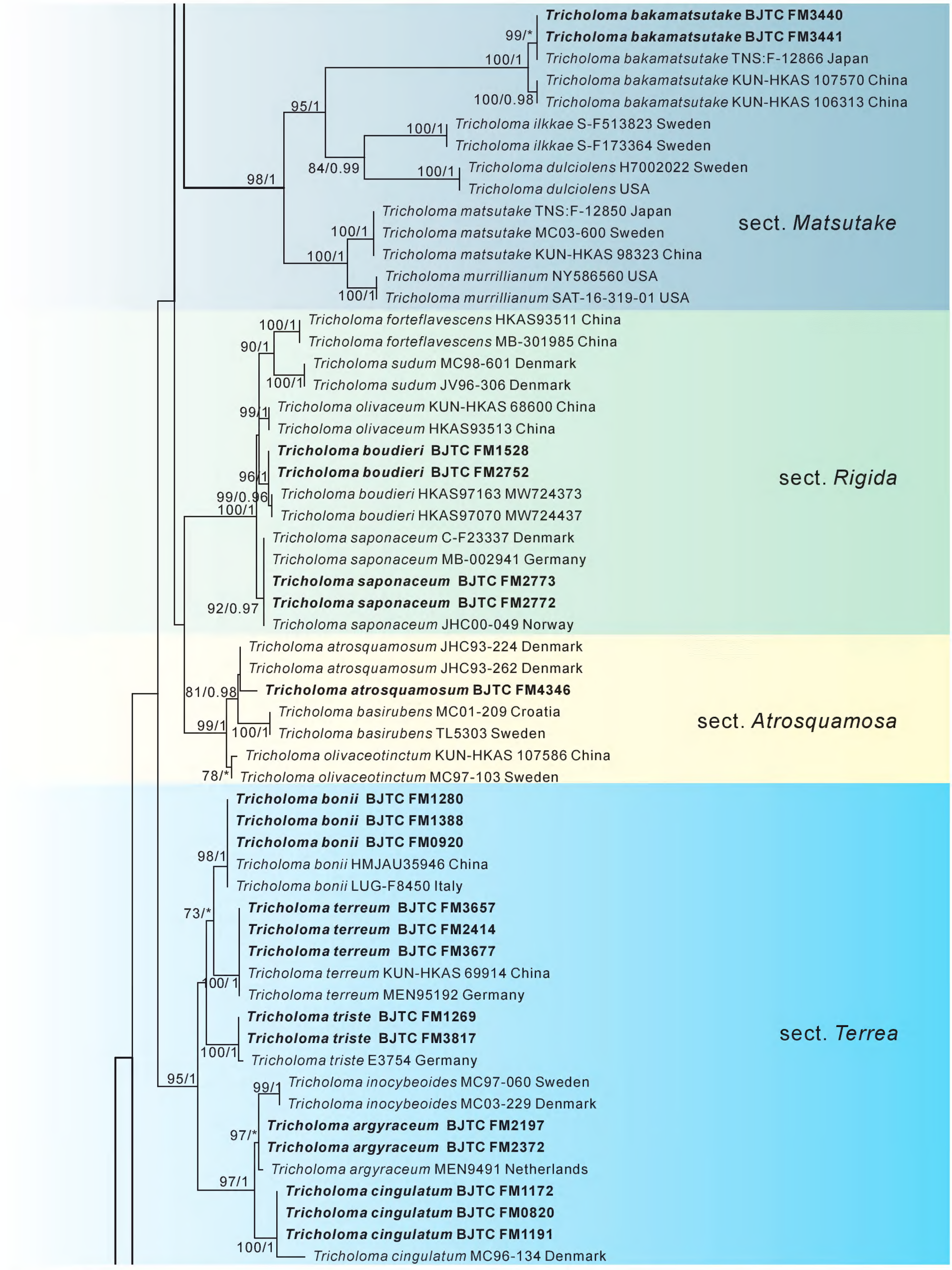

Figure 1. Continued.

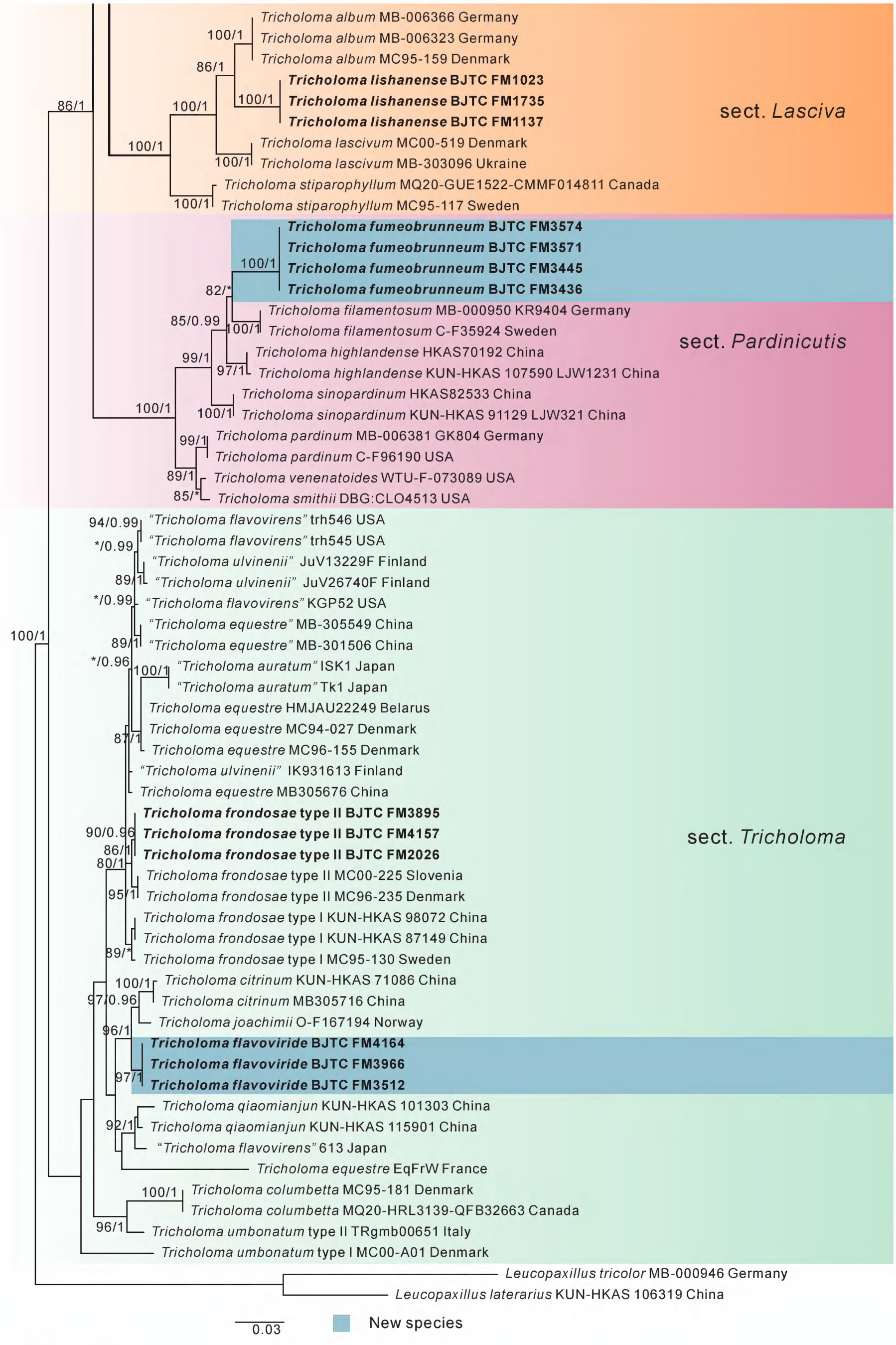
Tricholoma album MB-006366 Germany
Tricholoma album MB-006323 Germany
Tricholoma album MC95-159 Denmark
***Tricholoma lishanense* BJTC FM1023**
***Tricholoma lishanense* BJTC FM1735**
***Tricholoma lishanense* BJTC FM1137**
Tricholoma lascivum MC00-519 Denmark
Tricholoma lascivum MB-303096 Ukraine
Tricholoma stiparophyllum MQ20-GUE1522-CMMF014811 Canada
Tricholoma stiparophyllum MC95-117 Sweden
sect. *Lasciva*
***Tricholoma fumeobrunneum* BJTC FM3574**
***Tricholoma fumeobrunneum* BJTC FM3571**
***Tricholoma fumeobrunneum* BJTC FM3445**
***Tricholoma fumeobrunneum* BJTC FM3436**
Tricholoma filamentosum MB-000950 KR9404 Germany
Tricholoma filamentosum C-F35924 Sweden
Tricholoma highlandense HKAS70192 China
Tricholoma highlandense KUN-HKAS 107590 LJW1231 China
Tricholoma sinopardinum HKAS82533 China
Tricholoma sinopardinum KUN-HKAS 91129 LJW321 China
Tricholoma pardinum MB-006381 GK804 Germany
Tricholoma pardinum C-F96190 USA
Tricholoma venenatoides WTU-F-073089 USA
Tricholoma smithii DBG:CLO4513 USA
sect. *Pardinicutis*
"*Tricholoma flavovirens*" trh546 USA
"*Tricholoma flavovirens*" trh545 USA
"*Tricholoma ulvinenii*" JuV13229F Finland
"*Tricholoma ulvinenii*" JuV26740F Finland
"*Tricholoma flavovirens*" KGP52 USA
"*Tricholoma equestre*" MB-305549 China
"*Tricholoma equestre*" MB-301506 China
"*Tricholoma auratum*" ISK1 Japan
"*Tricholoma auratum*" Tk1 Japan
Tricholoma equestre HMJAU22249 Belarus
Tricholoma equestre MC94-027 Denmark
Tricholoma equestre MC96-155 Denmark
"*Tricholoma ulvinenii*" IK931613 Finland
Tricholoma equestre MB305676 China
***Tricholoma frondosae* type II BJTC FM3895**
***Tricholoma frondosae* type II BJTC FM4157**
***Tricholoma frondosae* type II BJTC FM2026**
Tricholoma frondosae type II MC00-225 Slovenia
Tricholoma frondosae type II MC96-235 Denmark
Tricholoma frondosae type I KUN-HKAS 98072 China
Tricholoma frondosae type I KUN-HKAS 87149 China
Tricholoma frondosae type I MC95-130 Sweden
Tricholoma citrinum KUN-HKAS 71086 China
Tricholoma citrinum MB305716 China
Tricholoma joachimii O-F167194 Norway
***Tricholoma flavoviride* BJTC FM4164**
***Tricholoma flavoviride* BJTC FM3966**
***Tricholoma flavoviride* BJTC FM3512**
Tricholoma qiaomianjun KUN-HKAS 101303 China
Tricholoma qiaomianjun KUN-HKAS 115901 China
"*Tricholoma flavovirens*" 613 Japan
Tricholoma equestre EqFrW France
Tricholoma columbetta MC95-181 Denmark
Tricholoma columbetta MQ20-HRL3139-QFB32663 Canada
Tricholoma umbonatum type II TRgmb00651 Italy
Tricholoma umbonatum type I MC00-A01 Denmark
sect. *Tricholoma*
Leucopaxillus tricolor MB-000946 Germany
Leucopaxillus laterarius KUN-HKAS 106319 China
0.03
New species

Figure 1. Continued.

Figure 2. Photographs of basidiomata in their natural habitat **A, B** *Tricholoma flavoviride* (**A** BJTC FM3996, **B** BJTC FM4164) **C, D** *T. fumeobrunneum* (**C** BJTC FM3571, **D** BJTC FM3574) **E, F** *T. parafulvum* (**E** BJTC FM2500, **F** BJTC FM4065) **G, H** *T. viscidum* (**G** BJTC FM4038, **H** BJTC FM4198). Scale bars: 1 cm.

Basidiospores [90/3/3] 5–6.5 × 3.5–5 µm, Q = 1.2–1.6, ellipsoid, smooth, inamyloid, usually containing one large oil droplet. ***Basidia*** 24–37 × 5.5–7.5 µm, clavate, (2–)4-spored, sterigmata up to 4.5 µm long. ***Cystidioid cells*** in hymenium absent. ***Hymenophoral trama*** regular, composed of cylindrical hyphae, 4–10 µm wide, colorless in water and 5% KOH. ***Pileipellis*** a cutis, composed of cylindrical hyphae, 4–10 µm wide, colorless or yellowish in water and 5% KOH. ***Stipitipellis*** a cutis, composed of parallel hyphae, 2–6 µm wide, colorless in water and 5% KOH. ***Clamps*** absent in all tissues.

Ecology and habitat. Scattered or gregarious on the ground in broadleaf forest dominated by *Quercus* sp., currently only known from Shanxi Province, northern China.

Additional specimens examined. China • Shanxi Province, Pu County, Wulu Mountain, on the ground in broadleaf forest dominated by *Quercus* sp., 28 September 2023, J.Z Cao, CF2196 (BJTC FM3966), GenBank Acc. No.: ITS = PQ499559, mtSSU = PQ499563, *rpb2* = PQ509906, *mcm7* = PQ509916; ibid., Qinshui County, Lishan Mountain, on the ground in broadleaf forest dominated by *Quercus* sp., 7 September 2023, N. Mao, MNM829 (BJTC FM3512), GenBank Acc. No.: ITS = PQ499561, mtSSU = PQ499562, *rpb2* = PQ509905, *mcm7* = PQ509915.

Notes. *Tricholoma flavoviride* belongs to the sect. *Tricholoma* (Fig. 1). *Tricholoma citrinum*, a species recently described from Yunnan Province of southwestern China (Cui et al. 2022), is morphologically and phylogenetically closely related to the new species. Both species have brownish-yellow pileus and ellipsoid basidiospores. However, *T. citrinum* is distinguished from *T. flavoviride* by its relatively paler pileus, stipe sometimes smooth, and habitat association with pine forests. Morphologically, *T. flavoviride* is also easily confused with *T. equestre* (L.) P. Kumm., and *T. frondosae* Kalamees & Shchukin. *Tricholoma equestre* is distinguished from *T. flavoviride* by its larger basidiospores (6.5–9 × 4–5.5 µm) and habitat associated with pine forests; *T. frondosae* by its paler pileus and larger basidiospores (7–8.5 × 4–5 µm) (Christensen and Heilmann-Clausen 2013; Reschke et al. 2018; Cui et al. 2022).

Tricholoma fumeobrunneum L. Fan, N. Mao & J.J Yang, sp. nov.

MycoBank No: MB 856306

Figs 2C, D, 3B, D

Diagnosis. It is distinguished by the combination of the following features: pale gray to grayish-brown pileus, smooth stipe, and broadly ellipsoid to ellipsoid basidiospores. It is most similar to *T. sinopardinum* Zhu L. Yang, X.X. Ding, G. Kost & Rexer but differs by the smaller basidiospores (6.5–8.5 × 5–6.5 µm).

Holotype. China • Shanxi Province, Lingchuan County, Lishan Mountain, 35°36'6"N, 113°20'32"E, elev. 1185 m, on the ground in broadleaf forest dominated by *Quercus* sp., 28 August 2023, Y. Li, MS492 (BJTC FM3436), GenBank Acc. No.: ITS = PQ499553, mtSSU = PQ499565, *tef1-α* = PQ509897, *rpb2* = PQ509908, *mcm7* = PQ509918.

Etymology. *fumeobrunneum* (Lat.): referring to the cap color of the basidiomata.

Description. ***Basidiomata*** small to medium-sized. ***Pileus*** 25–77 mm diam., at first convex, later broadly convex, plano-convex to applanate with age, with an

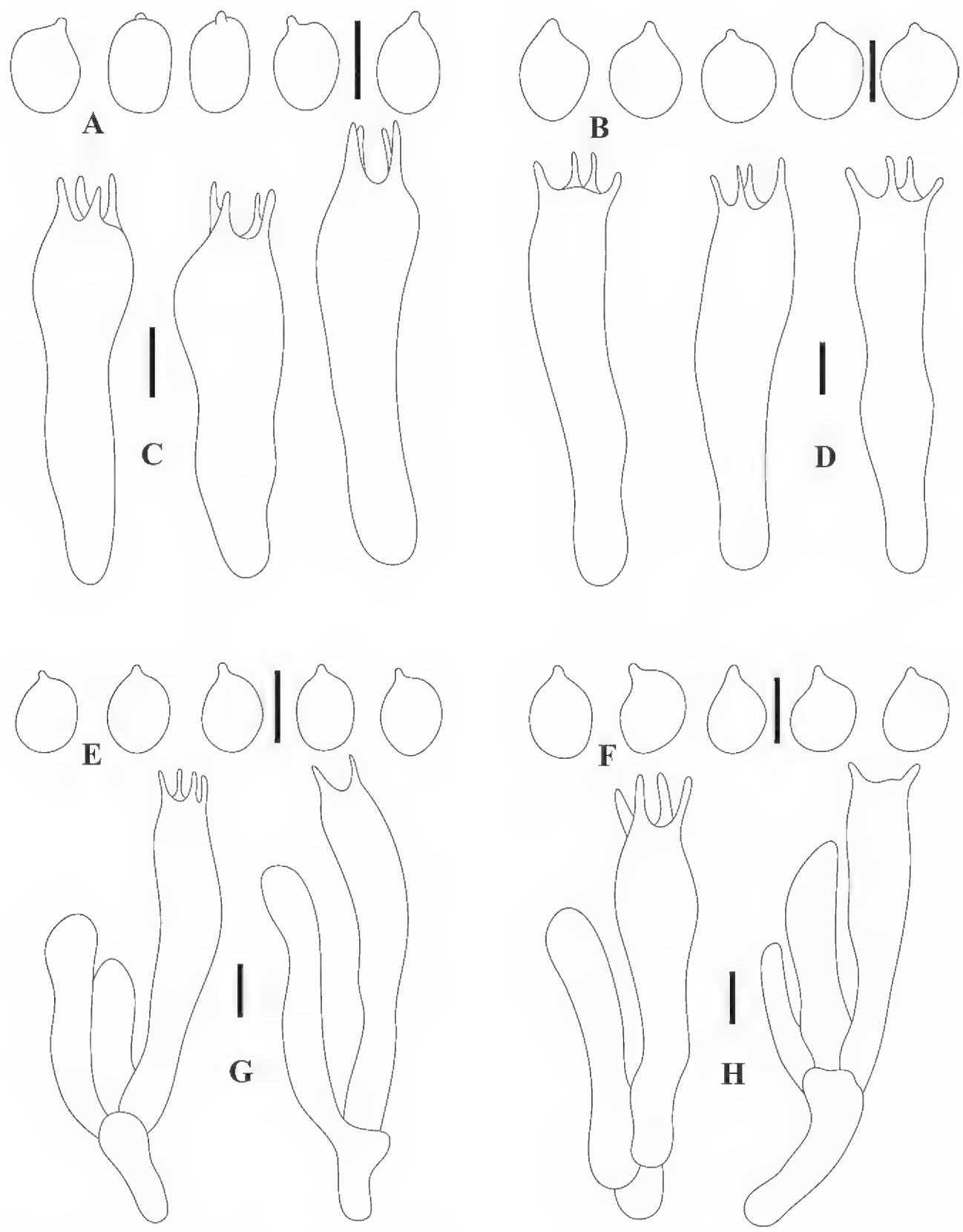

Figure 3. Microscopic features **A, C** *Tricholoma flavoviride* **B, D** *T. fumeobrunneum* **E, G** *T. parafulvum* **F, H** *T. viscidum* **A, B, E, F** basidiospores **C, D, G, H** basidia. Scale bars: 5 µm.

umbo at center; surface dry, pale gray (#cac7c0) to grayish-brown (#9d8166), center darker to dark gray (#aaa9a3) to grayish black (#6b6157) when mature, covered with dark gray (#8e8c95) reflexed fibrillose squamules; margin at first involute, later incurved, cracking with age. ***Lamellae*** sinuate, moderately crowded, dirty white (#f9f8e9) to pale yellow (#f1eeca), turning yellowish brown (#e7dbb2) to brown (#d6bb9c) with age; lamellulae in 2–4 tiers, concolorous with lamellae. ***Stipe*** 50–76 mm long, 7–15 mm diam., cylindrical to clavate, enlarged downwards, dry, white (#f6f7f7), pale yellow (#f1ffe3) to yellowish brown (#ab9065), smooth. ***Context*** white (#f9f9f9), up to 3.3 mm. ***Odor*** unrecorded. ***Taste*** not recorded.

Basidiospores [120/3/4] 6.5–8.5 × 5–6.5 µm, Q = 1.3–1.6, broadly ellipsoid to ellipsoid, smooth, inamyloid, usually containing one large oil droplet. ***Basidia*** 34–46 × 6–9 µm, clavate, (2–)4-spored, sterigmata up to 6 µm long. ***Cystidioid cells*** in hymenium absent. ***Hymenophoral trama*** regular, composed of cylindrical hyphae, 3–12 µm wide, colorless in water and 5% KOH. ***Pileipellis*** a cutis, composed of cylindrical hyphae, 3–10 µm wide, colorless or yellowish-brown in water and 5% KOH. ***Stipitipellis*** a cutis, composed of parallel hyphae, 1.5–6 µm wide, colorless in water and 5% KOH. ***Clamps*** common in all tissues.

Ecology and habitat. Scattered or gregarious on the ground in broadleaf forest dominated by *Quercus* sp., currently only known from Shanxi Province, northern China.

Other specimens examined. CHINA • Shanxi Province, Lingchuan County, Lishan Mountain, on the ground in broadleaf forest dominated by *Quercus* sp., 5 September 2023, N. Mao, MNM891 (BJTC FM3571), GenBank Acc. No.: ITS = PQ499554; ibid., Lingchuan County, Lishan Mountain, 35°36'6"N, 113°20'32"E, elev. 1190 m, on the ground in a broadleaf forest dominated by *Quercus* sp., 28 August 2023 H.M. Ji, MS492 (BJTC FM3445), GenBank Acc. No.: ITS = PQ499552, mtSSU = PQ499566, *tef1-α* = PQ509898, *rpb2* = PQ509909, *mcm7* = PQ509919; ibid., 5 September 2023, N. Mao, MNM894 (BJTC FM3574), GenBank Acc. No.: ITS = PQ499555, mtSSU = PQ499567, *tef1-α* = PQ509899, *mcm7* = PQ509920.

Notes. *Tricholoma fumeobrunneum* belongs to the sect. *Pardinicutis* (Fig. 1). *Tricholoma fumeobrunneum* was phylogenetically sister to *T. sinopardinum*, a species found in Xizang Autonomous, southwestern China. However, *T. sinopardinum* differs from the new species by its stipe covered with brownish, brown to dark brown fibrillose to reflexed squamules and larger basidiospores (8.5–10.5 × 6.5–7.5 µm) (Yang et al. 2017). *Tricholoma highlandense* Zhu L. Yang, X.X. Ding, G. Kost & Rexer, another species from China in this section, is easily distinguished from *T. fumeobrunneum* by its pileus without a tinge of gray and occurrence in red acid soil (Yang et al. 2017).

Tricholoma parafulvum **L. Fan, N. Mao & J.J Yang, sp. nov.**

MycoBank No: MB 856307

Figs 2E, F, 3E, G

Diagnosis. It is distinguished by the combination of the following features: yellowish brown, brown to dark brown pileus, stipe surface covered with brown fibrils, and broadly ellipsoid to ellipsoid basidiospores. It is most similar to *Tricholoma fulvum* (DC.) Bigeard & H. Guill. but differs in the pileus surface without being radially streaky.

Holotype. CHINA • Shanxi Province, Qinshui County, Lishan Mountain, 35°36'5"N, 113°20'29"E, elev. 1600 m, on the ground in broadleaf forest dominated by *Quercus* sp., 5 October 2023, J.Z. Cao, CF2300 (BJTC FM4065), GenBank Acc. No.: ITS = PQ499537, mtSSU = PQ499568, *tef1-α* = PQ509900, *rpb2* = PQ509910, *mcm7* = PQ509921.

Etymology. *Parafulvum* (Lat.): referring to the fact that the new species is very similar to *Tricholoma fulvum* in basidiomatal appearance.

Description. ***Basidiomata*** small to medium-sized. ***Pileus*** 30–66 mm diam., at first hemispherical to convex, later plano-convex to applanate with age, with depression or an umbo at center; surface dry, slightly viscid when wet, yellowish brown (#edd6b8), brown (#d49d76) to dark brown (#b78877), darker in the center and paler towards the margin, covered with brown (#a1735b) to dark brown (#845546) reflexed fibrillose squamules; margin at first involute, later incurved, cracking with age. ***Lamellae*** sinuate, moderately crowded, yellow (#f3edd7) to yellowish brown (#ddb68b) when young, turning dark brown (#c1986e) with age; lamellulae in 2–3 tiers, concolorous with lamellae. ***Stipe*** 42–83 mm long, 5–22

mm diam., cylindrical to clavate, enlarge downwards, dry, white (#f5fae3), yellowish brown (#c1a36f) to brown (#9d7963), covered with brown (#7e5c43) fibrils. ***Context*** white (#f7f8f7), up to 11 mm. ***Odor*** unrecorded. ***Taste*** not recorded.

Basidiospores [90/3/3] 4.5–6 × 3.5–4.5 µm, Q = 1.3–1.4, broadly ellipsoid to ellipsoid, smooth, inamyloid, usually containing one large oil droplet. ***Basidia*** 23–37 × 4.5–7 µm, clavate, (2–)4-spored, sterigmata up to 5.5 µm long. ***Cystidioid cells*** in hymenium absent. Hymenophoral trama regular, composed of cylindrical hyphae, 3–7 µm wide, colorless in water and 5% KOH. ***Pileipellis*** a cutis,

Figure 4. Photographs of basidiomata in their natural habita **A, B** *Tricholoma ammophilum* (HSA 371) **C** *T. argyraceum* (BJTC FM3571) **D** *T. aurantium* (BJTC FM2195) **E** *T. bakamatsutake* (BJTC FM3441) **F** *T. bonii* (BJTC FM905) **G** *T. boudieri* (BJTC FM2752) **H** *T. cingulatum* (BJTC FM1172) **I** *T. frondosae* (BJTC FM3895) **J** *T. imbricatum* (BJTC FM1170) **K** *T. lishanense* (BJTC FM1735) **L** *T. populinum* (BJTC FM1144). Scale bars: 1 cm.

composed of cylindrical hyphae, 3–8 µm wide, colorless or yellowish-brown in water and 5% KOH. ***Stipitipellis*** a cutis, composed of parallel hyphae, 2–7 µm wide, colorless in water and 5% KOH. ***Clamps*** absent in all parts of basidioma.

Ecology and habitat. Scattered or gregarious on the ground in broadleaf forest dominated by *Quercus* sp. or *Betula* sp., currently only known from Shanxi Province, northern China.

Additional specimens examined. China • Shanxi Province, Qinshui County, Lishan Mountain, on the ground in broadleaf forest dominated by *Quercus* sp., 5 October 2023, J.Z. Cao, MS855 (BJTC FM4210), GenBank Acc. No.: ITS = PQ499538, mtSSU = PQ499569, *tef1-α* = PQ509901, *rpb2* = PQ509911, *mcm7* = PQ509922; ibid., Loufan County, Yundingshan Mountain, on the ground in broadleaf forest dominated by *Betula* sp., 23 August 2022, N. Mao, MNM738 (BJTC FM2500), GenBank Acc. No.: ITS = PQ499536.

Notes. *Tricholoma parafulvum* belongs to sect. *Genuina* (Fig. 1). *Tricholoma fulvum* is morphologically similar and phylogenetically closely related to the new species. They all have brownish caps and ellipsoid basidiospores. However, *T. fulvum* differs from *T. parafulvum* by its pileus with radially streaky and relatively larger spores (5.8–7.2 × 4.6–5.1 µm) (Christensen and Heilmann-Clausen 2013). Four species from this section are also found in Shanxi Province, i.e., *Tricholoma aurantium*, *T. ammophilum*, *T. populinum* and *T. viscidum*. Of them, *Tricholoma viscidum* is similar to *T. parafulvum*, both of which are associated with *Quercus* spp. However, *T. viscidum* differs from *T. parafulvum* by its pileus being extremely viscid when wet and relatively larger spores (5–6.5 × 4.5–5.5 µm). The remaining three species are easily distinguished from *T. parafulvum*, *T. ammophilum* and *T. populinum* by their habitats associated with *Populus* spp., *T. aurantium* by its stipe surface covered with dense, orange to brownish orange scaly (Heilmann-Clausen et al. 2017).

Tricholoma viscidum **L. Fan, N. Mao & J.J Yang, sp. nov.**

MycoBank No: MB 856308

Figs 2G, H, 3F, H

Diagnosis. It is distinguished by the combination of the following features: pileus surface viscid when wet, stipe surface covered with brown to dark brown fibrils, and broadly ellipsoid basidiospores. It is most similar to *T. ustaloides* Romagn. but differs in the absence of a sharply defined zone of white color on the upper part of the stipe surface.

Holotype. China • Shanxi Province, Qinshui County, Lishan Mountain, 35°29'8"N, 113°1'19"E, elev. 1658 m, on the ground in broadleaf forest dominated by *Quercus* sp., 29 September 2023, J.Z. Cao, MS843 (BJTC FM4198), GenBank Acc. No.: ITS = PQ499539, mtSSU = PQ499571, *tef1-α* = PQ509903, *rpb2* = PQ509913, *mcm7* = PQ509924.

Etymology. *viscidum* (Lat.): referring to the viscid cap of basidiomata when wet.

Description. ***Basidiomata*** small, medium to large-sized. ***Pileus*** 33–86 mm diam., at first hemispherical to convex, later plano-convex with age, with an umbo at center; surface viscid when wet, yellowish brown (#e6d3b8), brown (#d0b79d) to reddish brown (#9d6463), darker in the center and paler towards the margin, covered with brown (#ab7d6b) fibrils; margin at first involute, later incurved, cracking with age. ***Lamellae*** sinuate, crowded, dirty white (#f3fbd0) to

Figure 5. Photographs of basidiomata in their natural habitat **A** *Tricholoma psammopus* (BJTC FM814) **B** *T. saponaceum* (BJTC FM2773) **C** *T. atrosquamosum* (BJTC FM4346) **D** *T. terreum* (HSA 419) **E** *T. triste* (BJTC FM3817) **F** *T. vaccinum* (BJTC FM943). Scale bars: 1 cm.

pale yellow (#f1ffb8), turning brown (#c09a7e) with age; lamellulae in 2–3 tiers, concolorous with lamellae. ***Stipe*** 49–113 mm long, 10–18 mm diam., cylindrical to clavate, enlarged downwards, dry, yellowish brown (#c79f5c) to brown (#9f6327), covered with brown (#b99976) to dark brown (#8b6c68) fibrils. ***Context*** white (#f3eeea), up to 13 mm. ***Odor*** unrecorded. ***Taste*** not recorded.

Basidiospores [120/3/4] 5–6.5 × 4.5–5.5 µm, Q = 1.1–1.25, broadly ellipsoid to ellipsoid, smooth, inamyloid, usually containing one large oil droplet. ***Basidia*** 28–37 × 5–8 µm, clavate, (2–)4-spored, sterigmata up to 5.5 µm long. ***Cystidioid cells*** in hymenium absent. ***Hymenophoral trama*** regular, composed of cylindrical hyphae, 5–10.5 µm wide, colorless in water and 5% KOH. ***Pileipellis*** a cutis, composed of cylindrical hyphae, 4–9.5 µm wide, yellowish-brown in water and 5% KOH. ***Stipitipellis*** a cutis, composed of parallel hyphae, 2.5–6 µm wide, colorless in water and 5% KOH. ***Clamps*** absent in tissues.

Ecology and habitat. Scattered or gregarious on the ground in broadleaf forest dominated by *Quercus* sp., currently only known from Shanxi Province, northern China.

Additional specimens examined. CHINA • Shanxi Province, Qinshui County, Lishan Mountain, on the ground in broadleaf forest dominated by *Quercus* sp., 5 October 2023, J.Z. Cao, CF2268 (BJTC FM4038), GenBank Acc. No.: ITS = PQ499541; ibid., 29 September 2023, J.Z. Cao, MS844 (BJTC FM4199), GenBank Acc. No.: ITS = PQ499542, mtSSU = PQ499572, *tef1-α* = PQ509904, *rpb2* = PQ509914, *mcm7* = PQ509925; ibid., 25 August 2023, H.M. Ji MS443 (BJTC FM3388), GenBank Acc. No.: ITS = PQ499540, mtSSU = PQ499570, *tef1-α* = PQ509902, *rpb2* = PQ509912, *mcm7* = PQ509923.

Notes. *Tricholoma viscidum* belongs to the sect. *Genuina* (Fig. 1). *Tricholoma ustaloides* is closely related to the new species in morphology and phylogeny. They all have ellipsoid basidiospores and are associated with the *Quercus* spp. However, *T. ustaloides* differs from *T. viscidum* by its upper part of the stipe decorated with a distinctly and sharply delimited zone (Christensen and Heilmann-Clausen 2013; Halama et al. 2016). *Tricholoma ustale* (Fr.) P. Kumm., a European species often associated with *Fagus* spp. and *Carpinus* spp., is also easily confused with the new species as there are some reports that it is related to *Quercus* forests. However, *T. ustale* differs by its stipe flesh turning reddish brown when cut or bruised and its phylogenetic position (Christensen and Heilmann-Clausen 2013).

Discussion

Shanxi Province is located in northern China, where the climate ranges from subtropical to cold temperate. A total of 21 species of *Tricholoma* were confirmed in Shanxi Province in this study (Figs 1–5) based on morphological and molecular data, including four new species described in this paper. They are *T. ammophilum* A.D. Parker, Grubisha & S.A. Trudell, *T. argyraceum* (Bull.) Gillet, *T. atrosquamosum* Sacc., *T. aurantium* (Schaeff.) Ricken, *T. bakamatsutake* Hongo, *T. bonii* Basso & Candusso, *T. boudieri* Barla, *T. cingulatum* (Almfelt ex Fr.) Jacobasch, *T. flavoviride*, *T. frondosae*, *T. fumeobrunneum*, *T. imbricatum* (Fr.) P. Kumm., *T. lishanense* L. Fan & J.J. Yang, *T. parafulvum*, *T. populinum* J.E. Lange, *T. psammopus* (Kalchbr.) Quél., *T. saponaceum* (Fr.) P. Kumm., *T. terreum* (Schaeff.) P. Kumm, *T. triste* (Scop.) Quél., *T. vaccinum* (Schaeff.) P. Kumm., and *T. viscidum*. That means Shanxi Province is rich in species diversity of the genus *Tricholoma*.

Before the present study, there were nine *Tricholoma* species reported in Shanxi Province according to the related professional fungal literatures (Cao et al. 1990; Liu 1991; Mao 2000). Of them, five species are confirmed by the present study, including *T. argyraceum*, *T. cingulatum*, *T. populinum*, *T. terreum*, *T. vaccinum*. Of the remaining four species, *T. gambosum* is a species of

Calocybe currently as *Calocybe gambosa*, which is still not yet confirmed from this province; *T. matsutake* was reported based on the specimens under the tree of *Picea* sp. from Guancenshan Mountain in late 80th of last century (Cao et al. 1990). We are not able to examine the specimens cited by Cao et al. (1990), and also did not obtain new collections, so its occurrence is not confirmed; *T. virgatum* (Fr.) P. Kumm. was reported by Mao (2000), but no specimen was cited. According to the picture of basidiomata cited in his book, we suspect this name is probably misapplied for *T. bonii*; *T. zelleri* (D.E. Stuntz & A.H. Sm.) Ovrebo & Tylutki was reported by Liu (1991) from Qinshui County in southern Shanxi Province under *Pinus armandii* and *P. tabuliformis*, this name has already been treated as a synonym of *Tricholoma focale* (Fr.) Ricken by Kuo (2018). *Tricholoma focale* is a distinct species, that is morphologically very similar to the new species *T. viscidum* described in the present study, but we did not find it again for the time being.

Many species of *Tricholoma* have been observed having exclusively host association in Shanxi Province in this study; for example, both *T. bonii* and *T. psammopus* are associated with *Larix gmelinii* var. *principis-rupprechtii* only, *T. vaccinum* with *Picea* spp. only, *T. populinum* with *Populus* sp. only, *T. terreum* and *T. imbricatum* with *Pinus tabuliformis* only, some species, viz. *T. atrosquamosum*, *T. bakamatsutake*, *T. fumeobrunneum*, *T. lishanense* and *T. viscidum* with *Quercus* spp. only. A few species have a relatively wide host range. *Tricholoma cingulatum* grows under the trees of *Populus* spp. or *Quercus* sp., *T. aurantium* grows under *Quercus* sp. or *Picea* sp., *T. argyraceum* appears under *Pinus tabuliformis*, *P. sylvestris*, *Betula* sp. and *Quercus* sp. These host specificities are a useful guide for identifying the *Tricholoma* in the field.

The distribution of *Tricholoma* is significantly influenced by the geography of their host and the climate in Shanxi Province. There are two main geographic zones to be recognized in Shanxi Province: i) the subalpine zone with vegetation composed of coniferous *Larix-Picea* and broadleaf *Populus-Betula* and with a cold climate, which is mainly located in the mountain area above an altitude of 1600 m and some northern regions; ii) the warm zone with the vegetation composed of conifer's *Pinus* spp. and broadleaf *Quercus* spp. and with a warm climate, which is mapped in most of the central and southern Shanxi Province. Some *Tricholoma* species are only distributed in the subalpine zone, including *T. bonii*, *T. populinum*, *T. psammopus*, *T. triste* and *T. vaccinum*. Only a few species are observed appearing in both subalpine and warm zones, such as *T. argyraceum*, *T. aurantium*, and *T. cingulatum*. In contrast, the warm zone is rich in species of this genus, with at least 13 species found that are only distributed in this zone, including the most popularly encountered *T. terreum*, which is often confused with the northern *T. bonii*.

The climate also clearly shaped the geographic map of the *Tricholoma* species in this province. One of the good samples is the species *T. bonii*, an exclusive *Larix*-associated species in this province. It is the most popularly encountered mushroom in the forest of *Larix gmelinii* var. *principis-rupprechtii* in the northern region, but in the southern area, it is completely absent although there are many plantations of *L. gmelinii* var. *principis-rupprechtii* colonized for more than 50 years. Another example is *T. lishanense*, one of the most common *Tricholoma* in Lishan Mountain under *Quercus* spp.; its distribution is limited to Zhongtiao Mountains, where there are some subtropical climate areas.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

LF conceived and designed the study; NM wrote the manuscript and conducted phylogenetic analyses; NM and JJY conducted morphological observations; YXZ and LT conducted the experiments.

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Data availability

All of the data that support the findings of this study are available in the main text.

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